

# POLLEN-OVULE RATIOS, BREEDING SYSTEMS AND DISTRIBUTION PATTERNS OF SOME AUSTRALIAN GNAPHALIINAE (COMPOSITAE: INULEAE)

by

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## ABSTRACT

Pollen-ovule ratios (P/O's) were used to determine the breeding systems of 24 species in 13 genera of the subtribe Gnaphaliinae (Compositae: Inuleae). In many cases where P/O's were determined for 3 or more widely separated populations within a species P/O values were very uniform and species were readily classed as either outbreeders (P/O's = c.1,500-6,000) or inbreeders (P/O's = c.40-350). P/O variation between populations is discussed.

Changes from outbreeding to inbreeding were recognized in some closely related taxa of *Actinobole*, *Angianthus*, *Blennospora*, *Chrysocoryne*, *Chthonocephalus* and *Pogonolepis*. Character differences often associated with such changes include narrow vs wide distribution range, diploidy vs polyloidy, tetrasporangiate vs bisporangiate anthers and pentamerous vs tri- or tetramerous florets. Derived inbreeding taxa were generally widespread across much of Australia while their outbreeding congeners were restricted to parts of Western Australia. The data suggest that the inbreeding taxa originated in that state and subsequently spread eastwards. The salt lake systems of the south-west of Western Australia may have been important reservoirs from which colonization of the arid zone has occurred.

The following new combinations have been made: *Actinobole condensatum* (A. Gray) Short, *Blennospora phlegmatocarpa* (Diels) Short, *Pogonolepis muellerana* (Sond.) Short and *Siloxerous pygmaeus* (A. Gray) Short.

## INTRODUCTION

Cruden (1977), on the basis of data from 96 populations representing 80 species and approximately 30 families, has shown that pollen-ovule ratios (P/O's) are a good conservative indicator of a flowering plant's breeding system. Further data supporting the use of P/O's have been presented by Lloyd (1965), Baker (1967), Gibbs et al. (1975), Cruden (1976 a, b), Schoen (1977), Cruden and Hermmann-Parker (1979) and Spira (1980).

Merxmuller et al. (1977) drew attention to the lack of biosystematic studies in the Inuleae. In order to complement taxonomic revisions, P/O data, and thus breeding system data, have been determined for a number of endemic Australian taxa belonging to the tribe Inuleae (Compositae). Such data, along with chromosome number determinations, have led to a new understanding of the relationships and distribution patterns exhibited by many of the species and genera examined. It is hoped that the data obtained for the Compositae will be of interest to students of this family and workers in Australian biogeography and illustrate the value of P/O's in biosystematic and biogeographic studies.

Initial taxonomic investigations of the Inuleae by the present author were centred on members of the subtribe Angianthinae, one of nine subtribes recognised by Bentham (1873). Merxmuller et al. (1977) referred the majority of the members of the subtribe to an "*Angianthus* group" of the subtribe Gnaphaliinae. While the alignment of the various genera with others such as *Helichrysum* Miller and

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*Muelleria* 4(4): 395-417 (1981).

*Helipterum* DC. seems reasonable the group is nevertheless artificial, with genera being grouped together primarily because of their characteristic compound heads or glomerules. This condition occurs in a number of unrelated genera in the Compositae and is perhaps a result of selection for more efficient pollination or for a shorter life cycle. In the genera studied a reduction in life span is likely, many species being annuals living in arid or semi-arid conditions. In any case the Australasian "Angianthus group" contains genera which are probably not as closely related as current classification suggests, preliminary studies clearly indicating the need for critical revisions of the currently recognised genera of Gnaphaliinae. For example, studies in the genus *Angianthus* Wendl. (sensu Bentham, 1867) suggest that c.10 segregate genera should be recognized (Short, in press), a conclusion more or less in accord with a previous treatment of the Angianthinae by Gray (1851). Thus in this paper *Chrysocoryne* Endl., *Dithyrostegia* A. Gray, *Epitriche* Turcz., *Hyalochlamys* A. Gray, *Pogonolepis* Steetz and *Siloxerus* Labill. are recognised. Other genera of the "Angianthus group", e.g. *Actinobole* Fenzl ex Endl., *Blenhospora* A. Gray and *Chthonocephalus* Steetz, have also been examined and P/O distribution data are outlined for members of these genera plus various other taxa belonging to the subtribe Gnaphaliinae.

The subtribe Gnaphaliinae (sensu Merxmuller et al., 1977) consists of perhaps 95-100 genera and has a world-wide distribution, the main centres of diversity being in South America and Australia. Smaller centres occur in South Africa and the Mediterranean. Because of the artificiality of the "Angianthus group", elaboration of its general distribution is somewhat meaningless. However, in the sense of Merxmuller et al. (1977), the group is considered to be endemic to Australasia and it is of interest that many of the genera studied have their apparent centre of diversity in Western Australia. Indeed some, e.g. *Siloxerus* (3 spp.), *Cephalosorus* (1 sp.), *Dithyrostegia* (1 sp.), *Epitriche* (1 sp.) and *Hyalochlamys* (1 sp.) are endemic to the south-west of the state. The presence of some monotypic genera, of which relationships are at present obscure, suggests that some entities are relictual. This contrasts with the majority of taxa examined below, where it is suggested that at least the derived inbreeding species are probably of quite recent origin.

#### MATERIALS AND METHODS

To determine pollen-ovule ratios of hermaphroditic species all pollen grains were counted in a single floret taken from, usually, each of 15 individuals of a population. Whenever possible counts were obtained from 3 or more populations, all individual counts being combined to give an average P/O for the species.

To count pollen mature but indehiscent anthers were removed from florets and mounted in a solution of safranin or double stain (methyl green and phloxine: Owczarzac, 1952) and glycerin jelly. On squashing, mature anthers readily discharged their pollen grains which were then counted by using a grid in the eye piece of the microscope. The use of a cytoplasmic stain also enabled estimation of percentage pollen fertility although in the taxa examined no significant infertility was observed.

As there is a single ovule per floret in the Compositae the pollen-ovule ratio in hermaphroditic species is equal to the number of pollen grains per floret. To determine P/O's of andromonoecious and gynomonoeious taxa it was necessary to determine the ratio of male or female to bisexual florets. To accomplish this the number of bisexual and unisexual florets were counted in a single capitulum of each individual from which pollen was counted and the average percentages of unisexual and bisexual florets for a population were determined.

Voucher specimens of plants used for detailed pollen counts are housed in the State Herbarium of South Australia (AD).

Chromosome counts were obtained from either bud material fixed in the field or root tips obtained from freshly germinated seeds. A full account of the chromosome data will be published elsewhere.

Distribution maps have been compiled from specimens housed in the following herbaria (abbreviations after Holmgren and Keuken, 1974): AD, BRI, CANB, CBG, K, KP (Kings Park, Western Australia), MEL, NSW, NT, PERTH and UWA.

Several species found during the course of these studies are yet to be described and are referred to by capital letters, e.g. *Chrysocoryne* sp. A. Four new combinations have also been required (see appendix I). Thus *Calocephalus phlegmatocarpus* Diels has been transferred to *Blennospora* A. Gray, *Gnaphalodes condensatum* A. Gray to *Actinobole* Fenzl ex Endl., *Skirrhophorus muelleranus* Sond. to *Pogonolepis* Steetz and *Chamaesphaerion pygmaeus* A. Gray to *Siloxerus* Labill.

## RESULTS

Pollen-ovule data of species examined are summarised in table 1 and figure 1. Table 2 contains a summary of the character differences frequently found to occur between the closely related outbreeding and inbreeding species examined. Appendix 2 contains information pertaining to individual populations from which data were obtained while appendix 3 contains t-test results from paired comparisons of the P/O's of populations of each species.

Apart from andromonoecious *Helipterum pygmaeum* (DC.) Benth. and gynomonoeious *Helichrysum tepperi* F. Muell. all species examined in this paper are hermaphroditic and, with the exception of *Angianthus cunninghamii* (DC.) Benth., are annuals.

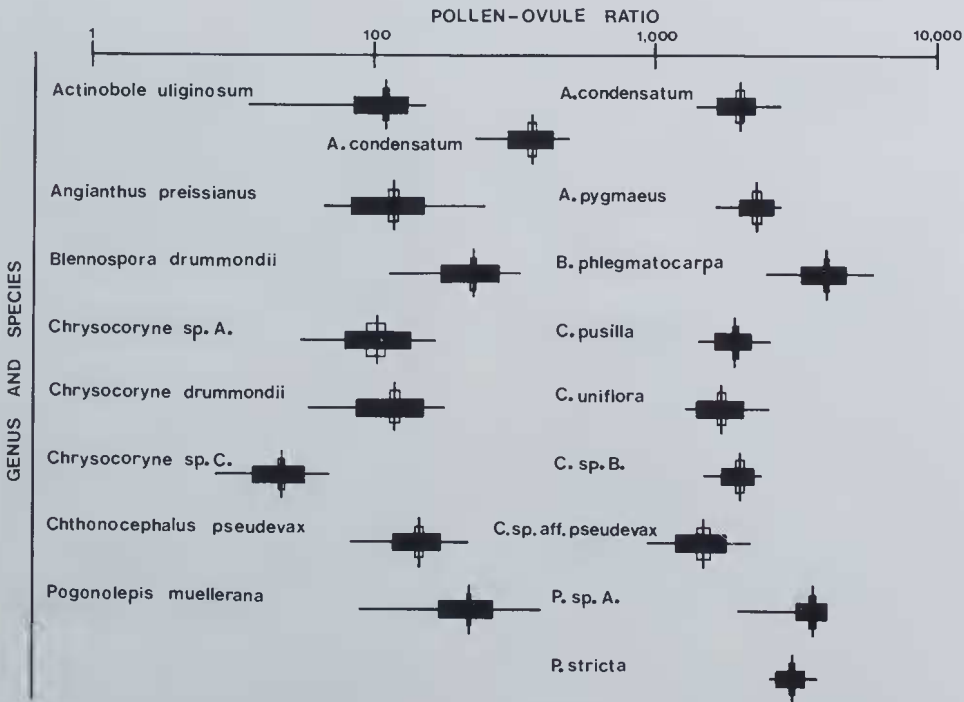


Fig. 1. Mean, range, standard deviation and standard error of pollen-ovule ratios of species of Gnaphaliinae.

Species	Pollen-ovule ratio				
	Mean	± Standard Deviation	± Standard Error	Number of individuals	Number of populations
<i>Actinobole condensatum</i>	2,037.4	357.4	68.7	27	2, 1 in part only
<i>Actinobole condensatum</i>	373.1	70.7	16.6	18	2, 1 in part only
<i>Actinobole uliginosum</i>	110.8	23.8	2.3	101	7
<i>Angianthus pygmaeus</i>	2,345.4	330.3	85.2	15	1
<i>Angianthus preissianus</i>	119.7	35.5	4.5	60	4
<i>Blennospora phlegmatocarpa</i>	4,119.7	762.4	113.6	45	3
<i>Blennospora drummondii</i>	231.0	53.7	6.2	75	5
<i>Chrysocoryne pusilla</i>	1,967.0	306.3	45.6	45	3
<i>Chrysocoryne sp.B.</i>	2,043.6	278.3	71.8	15	1
<i>Chrysocoryne uniflora</i>	1,777.5	354.1	91.4	15	1
<i>Chrysocoryne drummondii</i>	121.9	33.7	5.0	45	3
<i>Chrysocoryne sp.A.</i>	105.8	34.3	8.8	15	1
<i>Chrysocoryne sp.C.</i>	48.6	10.5	1.5	45	3
<i>Chthonocephalus sp. aff. pseudevax</i>	1,539.0	314.0	81.0	15	1
<i>Chthonocephalus pseudevax</i>	150.7	29.1	3.7	60	4
<i>Helipterum demissum</i>	84.6	18.1	3.3	30	2
<i>Millotia tenuifolia</i>	154.9	29.2	7.5	15	1
<i>Myriocephalus rhizocephalus</i>	107.6	23.1	5.9	15	1
<i>Pogonolepis stricta</i>	3,185.4	397.7	102.6	15	1
<i>Pogonolepis sp.A.</i>	3,761.4	516.7	133.4	15	1
<i>Pogonolepis muellerana</i>	227.2	51.8	5.4	90	6
<i>Rutidosis multiflora</i>	33.4	10.9	1.6	45	3
<i>Toxanthes muelleri</i>	86.0	19.4	5.0	15	1
<i>Helichrysum tepperi</i>	c. 37.5	—	—	15	1
<i>Helipterum pygmaeum</i>	c. 252	—	—	15	1

Table 1. Pollen-ovule ratios of species of Gnaphaliinae.

Outbreeder	Inbreeder	Species
High pollen-ovule ratio	Low pollen-ovule ratio	<i>Actinobole condensatum</i> / <i>A. uliginosum</i> <i>Angianthus pygmaeus</i> / <i>A. preissianus</i> <i>Angianthus drummondii</i> / <i>A. preissianus</i> <i>Blennospora phlegmatocarpa</i> / <i>B. drummondii</i> <i>Chrysocoryne</i> spp. <i>Chthonocephalus sp. aff. pseudevax</i> / <i>C. pseudevax</i> <i>Millotia</i> spp. <i>Pogonolepis</i> spp.
Anther sac long	Anther sac c. half as long	As above
Anthers tetrasporangiate	Anthers bisporangiate	As above
Florets pentamerous	Florets tri- or tetramerous	As above
Laminae of capitula bracts conspicuous	Laminae of capitular bracts less conspicuous	<i>Actinobole condensatum</i> / <i>A. uliginosum</i>
Inflorescence strongly scented	Inflorescence weakly scented	<i>Blennospora phlegmatocarpa</i> / <i>B. drummondii</i>
Protandrous	Protogynous	? <i>Blennospora phlegmatocarpa</i> / <i>B. drummondii</i>
Diploid	Polyloid	<i>Chrysocoryne</i> spp. <i>Pogonolepis</i> spp.
Restricted distribution	Wide distribution	<i>Actinobole condensatum</i> / <i>A. uliginosum</i> <i>Angianthus pygmaeus</i> / <i>A. preissianus</i> <i>Angianthus drummondii</i> / <i>A. preissianus</i> <i>Blennospora phlegmatocarpa</i> / <i>B. drummondii</i> <i>Chrysocoryne</i> spp. (p.p.) <i>Chthonocephalus sp. aff. pseudevax</i> / <i>C. pseudevax</i> <i>Pogonolepis</i> spp. (p.p.)

Table 2. Summary of character differences found to occur between related outbreeding and inbreeding species of Gnaphaliinae.

**Actinobole** Fenzl ex Endl.

This genus contains 2 species, *A. condensatum* (A. Gray) Short and *A. uliginosum* (A. Gray) Hj. Eichl. The former species is confined to Western Australia, occurring between latitudes c.24°S and 30°30'S and west of longitude c.116°E. It commonly grows in red sandy soil in open *Acacia-Ptilotus* shrubland but has also been collected on the coast, growing with *Carpobrotus*, *Calandrinia* etc. in white quartzite sand (Short 380). On the other hand the inbreeding *A. uliginosum*, with an average P/O = 110.8, is widely distributed across much of mainland Australia, occurring between latitudes c.22°S and c.38°S and west of longitude c.151°E (fig. 2). The species frequents a variety of habitats including granite outcrops, mallee scrub and the upper margins of salt lakes.

The capitular bracts of *A. condensatum* have larger laminae than those found in *A. uliginosum*. Differences in anther sac size and the occasional presence of tetramerous florets in *A. uliginosum* also reflect the different breeding systems displayed by the 2 species.

Both species of *Actinobole* possess an extremely efficient method of cypselas dispersal. The pappus in both species usually consists of 5-6 stiff bristles which, in the intact capitulum, lie parallel to the corolla tube. As the capitular bracts weaken at maturity the pappus bristles suddenly reflex, shooting the cypselas from the capitulum and dispersing them around the plant.

The most significant observation in the genus is the presence of 2 different P/O's within *A. condensatum*. The data suggest that northern populations of the species are primarily outbreeders with average P/O's of c.2,000. In contrast the southern populations sampled display an average P/O of several hundred. A single sample (Short 393) from a population located near the centre of the species distribution con-

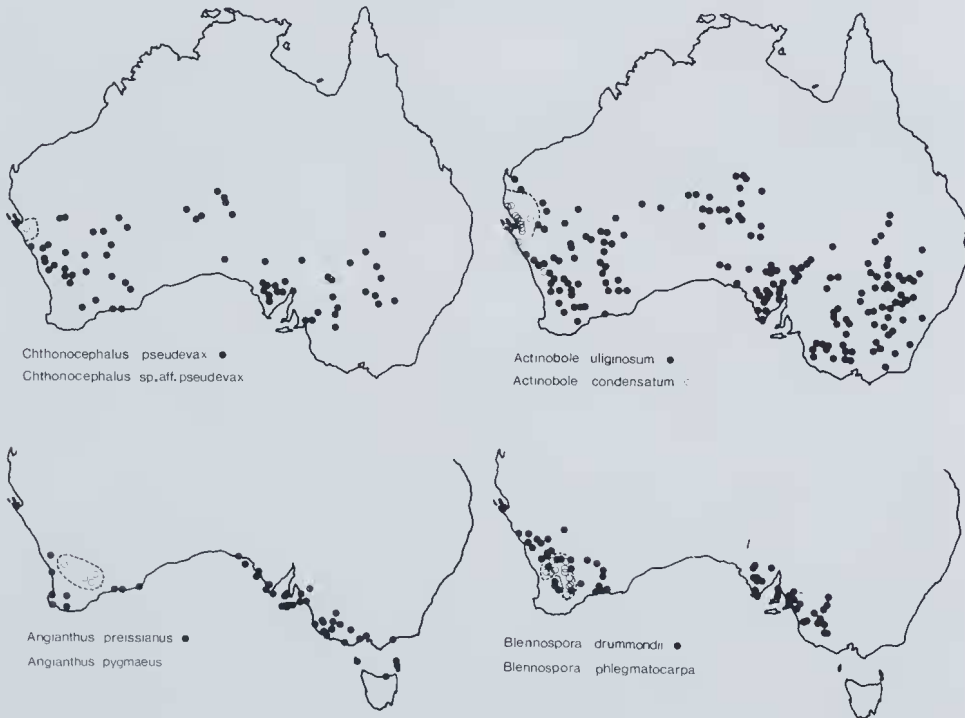


Fig. 2. Distribution of related outbreeding and inbreeding species of *Actinobole*, *Angianthus*, *Blennospora* and *Chthonocephalus*. Outbreeding species with open symbols, inbreeding species with closed symbols.





Fig. 3. Distribution of inbreeding (closed circles) and outbreeding (open circles) populations of *Actinobole condensatum* in Western Australia.

tains some individuals with high P/O's and others with low P/O's (fig. 3). P/O differences are correlated with changes in anther size but apart from this character no other differences are apparent between outbreeding and inbreeding individuals.

The distribution pattern observed within *A. condensatum* is reminiscent of patterns frequently displayed by diploid and tetraploid individuals. To date only a single chromosome count for the species,  $n=10$ , has been recorded (Turner, 1970). Turner's voucher collection, (T5388), contains specimens with high P/O's.

#### **Angianthus Wendl.**

Fifteen species are recognized within this genus (Short, in press). The majority of species have pentamerous florets but *A. preissianus* Steetz, with an average P/O of 119.7, has trimerous and tetramerous florets. Two species, *A. pygmaeus* (A. Gray) Benth and *A. drummondii* (Turcz.) Benth. (including specimens referred to *A. sp. aff. drummondii*, Short, in press) must be regarded as close relatives of *A. preissianus*. *A. drummondii* is an uncommon species and P/O data are unavailable. However, like *A. pygmaeus*, (with an average P/O of 2,345.4), the species contains pentamerous florets and from the few individuals examined, it appears that it too has a P/O of several thousand.

Both *A. pygmaeus* and *A. drummondii* are restricted to the south-west of Western Australia. The former species is restricted to saline depressions of the Avon River System (Bettenay and Mulcahy, 1972) between latitudes c.  $31^{\circ}30'S$  and  $33^{\circ}30'S$  and longitudes c.  $117^{\circ}00'E$  and  $120^{\circ}00'E$ . The only known specimens of *A. drummondii* are from the vicinity of the Tone, Hotham, Harvey and Preston Rivers. Specimens referred to as *A. sp. aff. drummondii* appear, like *A. pygmaeus*, to favour saline locations, most collections being from the Lake King-Lake Grace region of Western Australia. In contrast the inbreeding *A. preissianus* grows around salt lakes and along much of the coastline of southern mainland Australia and northern Tasmania (fig. 2).

Apart from differences in floret lobe number and anther sac size there is nothing to indicate the differences in breeding systems exhibited by *A. preissianus* and the related *A. pygmaeus* and *A. drummondii*.

Unlike the above-mentioned species of *Angianthus*, the remaining ones tend to produce large, showy compound heads and appear to have P/O's of one to several thousand. Some of the species, e.g. *A. acrohyalinus*, *A. milnei* and *A. tomentosus*, which are capable of producing compound heads containing perhaps 500 to c.2,000 two-flowered capitula, produce relatively few seeds under natural conditions. Thus even *A. tomentosus*, a species known to be self-compatible (G. J. Keighery, unpublished data), may only set c.100 seeds per compound head. The low actual: potential seed set ratio may be a reflection of selection for maintenance of a showy inflorescence, the prime purpose of which is to attract pollinators. In contrast to the outbreeders *A. preissianus* appears, as expected, to produce a full complement of apparently mature, viable seed.

Many species of *Angianthus* are endemic to, and have moderately restricted distributions in, Western Australia while species occurring in central and eastern Australia tend to be distributed over a much greater area of the continent (Short, in press). It is also noteworthy that eleven of the fifteen species often grow on the margin of salt lakes, with perhaps five or six being confined to such habitats. Several of these, including the only perennial species, *A. cunninghamii*, also occur in coastal situations.

#### **Blennospora** A. Gray

The genus *Blennospora* is considered here to contain 2 species, *B. drummondii* A. Gray and *B. phlegmatocarpa* (Diels) Short. These species, normally referred to *Calocephalus* R.Br., can be readily distinguished from that genus by a number of characters, i.e. pappus type, morphology and arrangement of bracts and cypsela morphology. *Calocephalus stowardii* Moore is considered to be conspecific with *B. phlegmatocarpa*.

*Blennospora phlegmatocarpa*, with an average P/O of 4,119.7, may be readily distinguished from its inbreeding relative, *B. drummondii*, (with an average P/O of 231), by its bright yellow, pentamerous florets and the presence of a strong, almost putrid odour. The latter species has brown pentamerous and occasionally tetramerous florets which emit a comparatively weak odour. Both species have a haploid chromosome number of 11.

Observations of style position at the time of dehiscence suggest that *B. phlegmatocarpa* is protandrous. In mature florets the style is exerted c.0.5-0.8 mm above the reflexed corolla lobes. However anthesis occurs well before the apparently immature style is exerted and indeed the majority of pollen is shed on the style as it grows between the anthers. The style arms remain straight as they pass between the anthers but reflex when growth stops. The high P/O and strong scent of the florets also suggests that the species is protandrous. This would be consistent with results obtained by Cruden (1977) for xenogamous species. Cruden (l.c.) also noted that the xenogamous species he examined were self-incompatible. This has not been checked in *B. phlegmatocarpa* but the recurved nature of the style arms suggests that in the event that cross-pollination does not occur the species may self-pollinate, some pollen always remaining in the floret after anthesis.

In *B. drummondii* recurved style arms are exerted above the corolla at anthesis but never as prominently as in *B. phlegmatocarpa*. The low P/O and the position of the style arms at anthesis suggest that the species is protogynous. This mechanism, despite the low number of pollen grains produced, would enable some outcrossing to occur. The species is self-compatible with most, if not all, florets appearing to produce mature, viable seed when pollinators are excluded.

*Blennospora phlegmatocarpa* is almost invariably restricted to the saline, often sandy, soils on the margins of salt lakes of the Avon River System (Bettenay & Mulcahy, 1972) between latitudes c.31°S and c.33°S and longitudes 116°E and

119°E (fig. 2). It is commonly associated with genera such as *Halosarcia*, *Atriplex* and *Disphyma*, all of which tend to grow in the innermost vegetation zone of salt lakes but occasionally individuals may be found in an outer *Melaleuca* zone. Although primarily restricted to salt lakes one collection (*Short 654*) has been made from *Eucalyptus* woodland near Bruce Rock and another (*Short 658*) from the base of granite rocks at Roe Dam.

*Blennospora drummondii* is a widespread species occurring in the south-west of Western Australia, southern South Australia and western Victoria (fig. 2). It undoubtedly has a much lower tolerance to salinity than *B.phlegmatocarpa* with only a few collections coming from the *Melaleuca* zone of salt lakes. Many collections of this species come from moss swards at the base of granite outcrops but it may be found in a range of woodland or mallee communities. The 2 species have never been found growing together.

### *Chrysocoryne* Endl.

This genus contains 6 species, namely *C.pusilla* (Benth.) Endl., *C.uniflora* Turcz. and *C.drummondii* A. Gray plus 3 new species, here referred to as *Chrysocoryne* spp. A, B and C. Three of the species are outbreeders while the remainder are inbreeders (table 1, fig. 1). All occur in the south-west of Western Australia (fig. 4), with only *C.pusilla* and *C.drummondii* extending beyond that state.

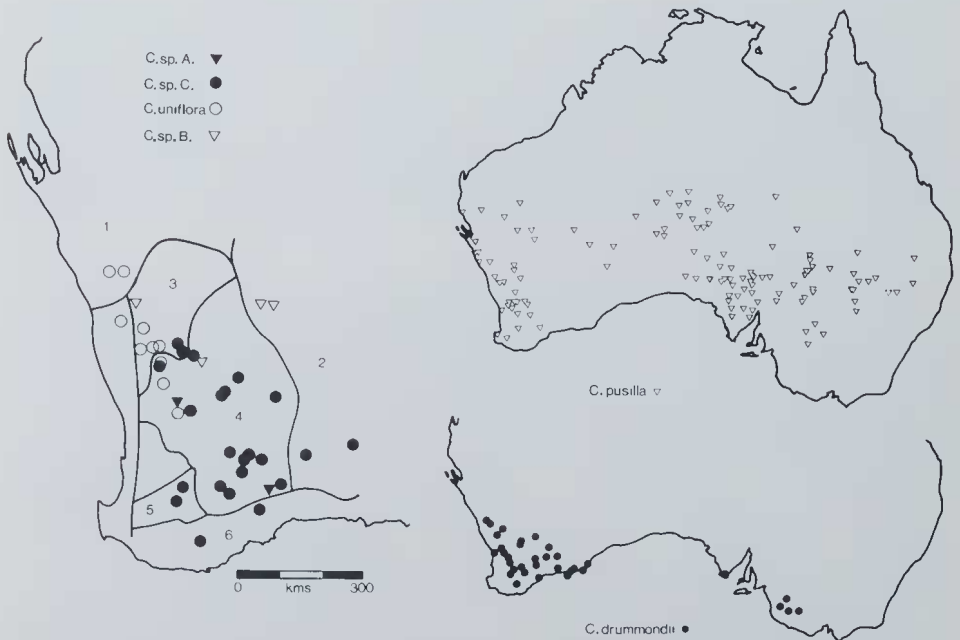


Fig. 4. Distribution of species of *Chrysocoryne*. Outbreeding species with open symbols, inbreeding species with solid symbols.

Drainage basins in Western Australia:

1. Murchison Division
2. Eucla Division
3. Monger System

4. Avon System
5. Blackwood System
6. South Coast System



Members of the genus are very closely related with differences occurring in the number of lobes per floret (inbreeders have predominantly, or entirely, tri- and tetramerous florets), the number of florets per capitulum, the number of capitular bracts per capitulum and the number of capitula per species. Differences in habit, bract morphology and chromosome numbers also occur and a tentative phylogeny has been constructed (Short, unpublished data). The outbreeding *C.pusilla* (average P/O = 1,967), a self-compatible species (G. J. Keighery, unpublished data), must be regarded as the species with the most primitive characteristics. Furthermore its distribution pattern contrasts with that observed in most other species examined in that it is an outbreeder widespread across much of Australia. Unlike the other species of *Chrysocoryne* it is also quite polymorphic. It frequents a wide range of habitats, commonly growing on the margins of saline depressions, on coastal dunes, in moss swards around granite outcrops, in chenopod steppe, or on *Triodia* dominated red sand-dunes of the inland.

The only other widespread species, the inbreeding *C.drummondii* (average P/O = 121.9), is generally morphologically uniform and occupies a number of habitats. In Western Australia it is confined to the south-west of the state, commonly occurring on the margins of salt lakes and at the base of granite outcrops. A few isolated populations occur on southern Eyre Peninsula, South Australia, while it is also common in a small region of south-eastern South Australia and central-western Victoria.

The remaining species, *C.uniflora* (average P/O = 1,777.5), B (average P/O = 2,043.6), A (average P/O = 105.8) and C (average P/O = 48.6), are restricted to salt lakes of Western Australia. Thus all species of *Chrysocoryne* may be encountered on the margins of saline depressions and indeed 2 or more commonly occur in the same locality. For example, all except species B have been collected from the saline Mortlock River flats near Meckering.

Specific differences are presumably maintained by a number of parameters, including differences in habitat, chromosome number and flowering time. Indeed *C.pusilla* is rarely observed growing amongst samphire, the common habitat of the other species, and tentative chromosome counts of  $n=6$ , 12 and  $c.13$  have been obtained for *C.pusilla* and species A and C respectively. Similarly field observations suggest that species C reaches maturity some days before the closely related *C.uniflora* with which it commonly grows. These factors, when combined with the inbreeding nature of 3 of the species, present a formidable barrier to interspecific crossing. No evidence of hybridization has been found between any species.

Mulcahy and Bettenay (1972) recognized 6 drainage divisions within Western Australia, and all species of *Chrysocoryne* occur within the South West Division. Both *C.pusilla* and *C.drummondii* are of course found both within and extensively outside the division. *Chrysocoryne uniflora* and species B and C are most common within the region while species A is in fact confined within its boundaries (fig. 4). A number of palaeo-drainage systems associated with the chains of salt lakes in the region may also be recognised within the division (Bettenay and Mulcahy, 1972). Species A is confined to the Avon System (fig. 4), the only collections coming from Lake King and the Mortlock River flats near Meckering. Although several collections come from both the southern edge of the Murchison Division and from the northern half of the Avon System, *C.uniflora* is undoubtedly most common in the Monger System. Species B, although extending into the Eucla Division where collections have been made from Lake Barlee, appears to be otherwise restricted to the upper half of the South West Division, single collections coming from the Monger and Avon Systems. Species C barely extends into the Monger System, being most common in the Avon, Blackwood and South Coast Systems. It has also been collected from two salt lakes in the south-west of the Eucla Division.

Thus it appears that the major drainage divisions and their constituent systems have influenced the distribution of species of *Chrysocoryne*. The occurrence of a species in more than one system is probably a reflection of the fact that seed disper-

sal, presumably by wind, is not inhibited by any substantial barriers, such as ranges of hills, between them.

The occurrence of all species on salt lakes is also reflected by the fact that they all possess scale-like glandular hairs on their stems and leaves, such hairs being characteristic of many plants growing in saline conditions. A few such hairs are always to be found on *C.pusilla* and *C.drummondii*, even when growing in non-saline habitats. This condition, plus their current distribution, strongly suggests evolution of the group in a saline environment.

### **Chthonocephalus Steetz**

This genus consists of perhaps 5 species, 3 of which are undescribed. Four of the species produce uniformly pentamerous florets while one, *C.pseudevax* Steetz has trimerous and tetramerous florets, an average P/O of 150.7, and is widespread across much of Australia, occurring between latitudes c.25°S and c.36°S and west of longitude c.148°E (fig. 2). It occupies a variety of habitats, commonly occurring in sandy depressions on granite outcrops or in sandy soil amongst *Halosarcia* and *Melaleuca* plants on the edge of saline depressions. The species is undoubtedly closely related to an undescribed, outbreeding species (average P/O = 1,539), here referred to as *C.sp.aff.pseudevax*. This taxon is known from a single collection (*Short 394*) coming from *Acacia linophylla*-dominated red sand-dunes c.100 km N. of the Murchison River Bridge on the North West Coastal Highway, Western Australia. Like *C.pseudevax* it is a dwarf, stemless plant, each plant having a single compound head, c.1-2 cm in diameter, surrounded by an involucre of leaves. The 2 species may be readily distinguished on leaf shape but *C.sp.aff.pseudevax*, because of its pentamerous florets, also has a much more conspicuous inflorescence than *C.pseudevax*.

Observations suggest that the 3 remaining species are predominantly outbreeders with P/O's of several thousand. Two of the species (*C.tomentellus* (F.Muell.) Benth. and *C.sp.aff.tomentellus* sp.nov.) are restricted to the Shark Bay region of Western Australia which contains all *Chthonocephalus* species and is the centre of diversity of the genus. The remaining species (undescribed) extends through much of central Western Australia and into the north-west of South Australia and the south-west of the Northern Territory.

### **Pogonolepis Steetz**

This genus contains a number of, as yet somewhat ill-defined, closely related outbreeding and inbreeding taxa. The genus has its centre of diversity in the south-west of Western Australia, where perhaps 6 taxa, all endemic, occur. A single species, *P.muellerana* (Sond.) Short, occurs in southern South Australia, southern New South Wales and Victoria. All taxa have pentamerous florets and their general appearance gives no reason to suspect the vast differences in P/O's obtained.

Three or four outbreeding taxa, including *P.stricta* (average P/O = 3,185.4) and *Pogonolepis* sp. A (Average P/O = 3,761.4), occur in Western Australia. To date accurate P/O's have not been determined but it is apparent that at least 2 inbreeding taxa also occur in that state, one taxon having only been collected from Eclipse Lake (*Chinnock 4357*). The remaining inbreeder, which appears to have close affinities with *P.muellerana*, is more widespread in southern Western Australia.

With the exception of *P.stricta*, which appears to be restricted to saline flats of Leschenault Inlet and the Vasse Estuary, all Western Australian taxa appear to occur on the margins of salt lakes and indeed several appear to be restricted to such habitats. The widespread *P.muellerana* (average P/O = 227.2) occupies a variety of habitats. It is extremely common amongst *Halosarcia* and other chenopods on the edge of both coastal and inland saline flats but is also common in a variety of mallee habitats.

Chromosome numbers promise to provide useful information in this genus. Counts of  $n = 4, 5$  and  $6$  have been obtained for outbreeding taxa, while counts of

$n=7$ ,  $c.10$  and  $c.12$  have been obtained for inbreeding taxa. The high numbers (i.e.  $c.10$  and  $12$ ) obtained for the presumably derived inbreeders suggests that at least two taxa are of polyploid origin.

#### **Millotia** Cass.

Schodde (1963, 1968) recognized 5 species of *Millotia*. Two species, *M. macrocarpa* Schodde and *M. tenuifolia* Cass. were found to possess trimerous and tetramerous florets while the remaining three, *M. myosotidifolia* (Benth.) Steetz, *M. greevesii* F. Muell, and *M. inopinata* Schodde have pentamerous florets. It was also found that the terminal anther appendages of the species with pentamerous florets were more or less exerted from the corolla tube at anthesis. In contrast the anthers of the other species were enclosed, or at least barely exposed, at anthesis. Such differences suggested to the present author that quite different breeding systems were likely to be found between species. Although adequate material was unavailable for detailed determinations of P/O's in all species, low P/O's occur in both *M. macrocarpa* and *M. tenuifolia*, an average P/O of 154.9 being recorded for the latter species. The remaining species appear to have P/O's of several thousand.

Of the inbreeders, *M. tenuifolia* is widespread across much of the southern Australian mainland and extends to Tasmania while *M. macrocarpa* occurs in semi-arid South Australia and north-western Victoria (Schodde, 1963). In contrast to the frequently observed patterns of distribution in related outbreeding and inbreeding species both *M. myosotidifolia* and *M. greevesii* are also widespread across much of Australia. On the other hand *M. inopinata* is restricted to more or less central Western Australia (Schodde, 1968).

#### **Siloxerus** Labill.

The members of this genus, *S. humifusus* Labill, *S. filifolius* (Benth.) Ostenf. and *S. pygmaeus* (A. Gray) Short are restricted to the south-west of Western Australia. Florets of the latter species are trimerous or tetramerous while both *S. humifusus* and *S. filifolius* have tetramerous and pentamerous florets. Good material for accurate P/O determinations was not available, but the few anthers examined suggest low P/O's ( $c.200$ ) for all species. A single specimen of *S. humifusus* (Short 1055) was found to have a P/O of 168.

*Siloxerus humifusus* is primarily distinguishable from *S. filifolius* on differences in the size of various organs, the cypselas, capitular bracts, pappus bristles and florets of *S. humifusus* being approximately twice the length of the same characters in the latter species. Such features suggest that *S. humifusus* may be of polyploid origin.

*Siloxerus humifusus* and *S. filifolius* occur in a variety of habitats, e.g. open *Eucalyptus*–*Xanthorrhoea* woodland or at the base of granite outcrops, and frequently occur together (fig. 5). On the other hand *S. pygmaeus*, occurring to the east and north of the other species, appears to grow almost exclusively on the margins of salt lakes of, mainly, the Avon System and the south-western section of the Eucla Division (Bettenay & Mulcahy, l.c.)

#### **Rutidosia** DC.

Usually nine or ten species are included in this-genus (Burbidge, 1963). A variety of characters, particularly of the cypselas, suggest that one, *R. multiflora* (Nees) Robinson, is generically distinct from the others. It possesses trimerous and tetramerous florets, has an average P/O of 33.4, and is widespread, occurring in Tasmania and across much of southern Australia.

#### **Toxanthes** Turcz.

Both species of this genus, *T. perpusilla* Turcz. and *T. muelleri* (Sond.) Benth., are widespread across southern Australia and usually have a mixture of trimerous, tetramerous and pentamerous florets in their capitula. The plants are small (several

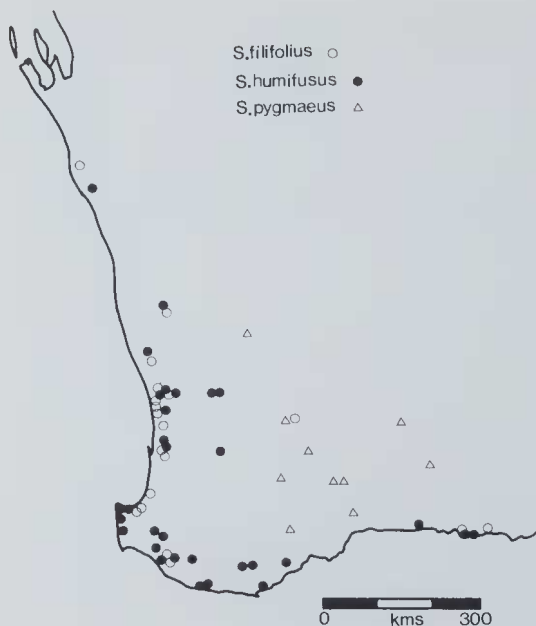


Fig. 5. Distribution of *Siloxerus* species in Western Australia.

cm high) and produce more or less inconspicuous capitula. P/O's have not been determined for *T. perpusilla* but, like *T. muelleri* (average P/O = 83.5), it should prove to be an inbreeding species.

The average P/O's of two other hermaphroditic species with tetramerous florets, *\*Myriocephalus rhizocephalus* (DC.) Benth. (average P/O = 107.6) and *Helipterum demissum* (A. Gray) Druce (average P/O = 84.6) have also been determined. Both species are inbreeders and are widespread across southern Australia, with *H. demissum* reaching Tasmania. Both *Myriocephalus* Benth. and *Helipterum* DC. are seriously in need of revision and no attempt has been made to determine the affinities of either species.

Gynomonoecious *Helichrysum tepperi* F. Muell. and andromonoecious *Helipterum pygmaeum* (DC.) Benth. are small, generally inconspicuous annuals and are widespread across southern Australia. *Helichrysum tepperi*, with an average P/O of 37.5, has a ratio of approximately 1 female to 1 bisexual floret. Both floret types are trimerous and tetramerous. *Helipterum pygmaeum*, with an average P/O of 252, produces from 3 to 5 florets per capitulum and has a ratio of approximately 1 male to 2 bisexual florets. The latter florets are tetra- or pentamerous while the male florets, the last formed, are tri-, tetra- or pentamerous. All florets produce approximately the same number of pollen grains.

## DISCUSSION

### Pollen-Ovule Ratios

As previously stated, Cruden (1977) has shown that P/O's are a conservative indicator of a flowering plant's breeding system, this conclusion also being supported in a number of other publications. Various factors can however result in a plant having a lower P/O than would normally be expected. For example a number of plants with clumped pollen, pollinia or polyads as in the Onagraceae, Asclepidaceae and Mimosaceae have much lower P/O's than those suggested by their apparent out-

\**M. isoetes* Diels is probably conspecific.



crossing attributes (Cruden, 1977; Cruden & Jensen, 1979). A further factor, asexual reproduction, may also be correlated with unexpectedly low P/O values in some plants. Thus in *Wurmbia dioica* (R.Br.) F. Muell. a polygamo-dioecious species of the Liliaceae which must usually, if not always, cross-pollinate, a seemingly low P/O of 818 (Short, unpublished data) may well be a reflection of this taxon's ability to produce bulbs.

However, despite the occasional exception there seems little doubt that P/O's do reflect a plant's breeding system. Indeed in the Gnaphaliinae examined very different P/O's were obtained for related species with obviously different morphological attributes which in themselves suggested different breeding systems, e.g. differences in bract size in *Actinobole condensatum* and *A. uliginosum*. Furthermore P/O's have also been very useful for distinguishing taxa almost unrecognizable by macro-morphological characters but with apparently distinctly different breeding systems from related taxa. Such examples are found in the various taxa of *Pogonolepis* and within *Actinobole condensatum*. In the latter species differences in P/O's obtained within a single population (Short 393) underline the importance of sampling individual plants within a population rather than obtaining a value from a mass sampling technique involving the lumping together of florets and/or anthers of more than one individual.

Few samples exist in the literature in which P/O's for a number of populations of a species have been determined. Where this has been the case the populations usually exhibit distinctly different P/O's which are reflected by various morphological characters and/or reproductive parameters such as pollinator activity and nectar production e.g. *Hedeoma hispida*, *Caesalpinia pulcherrima* (Cruden, 1976; Cruden & Hermman-Parker, 1979) and *Gilia achilleifolia* (Schoen, 1977). In the data presented (table I, appendix II) it is therefore significant that, with the exception of *Actinobole condensatum*, in cases where 3 or more apparently macro-morphologically similar populations were examined the P/O's were similar despite the large geographical range over which some species were sampled. That is, all populations of a species are readily referable to either a generalized inbreeding or outbreeding class.

On the other hand statistically different average P/O's occur between populations of many species (appendix II). For example in *Actinobole uliginosum* the average P/O's of the populations *Barker 2646* and *Short 377* are significantly different ( $p=0.001$ ) from the remaining populations of the species. In yet another case significantly different values were obtained in *Pogonolepis muellerana* where P/O values were determined for the same population in consecutive years (*Short 821*, *Short 870*,  $t=4.07$ ,  $p=0.001$ ). Given that the results reflect a true picture of P/O values then are the differences biologically significant?

Gene flow via pollen grain dispersal is influenced by parameters such as pollinator type and activity and the spacing of individual plants. Such factors make it difficult to draw any conclusions as to the significance of the P/O differences between populations. However it is worth recalling that even low levels of outcrossing may greatly affect the level of heterozygosity in a population. For example, although hybrid advantage probably influenced results, it is clear from experiments such as Allard's (1965) on lima beans that even a level of 5% outcrossing can greatly influence population structure. Furthermore Allard (l.c.) recorded that the degree of outcrossing in populations of wild oats may vary from c.1% to 10% and suggested that the degree of outcrossing is subject to ready adjustment. Perhaps then seemingly minor differences in pollen production reflect different degrees of recombination in populations.

The low P/O's of andromonoecious *Helipterum pygmaeum* (37.5) and gynomonoecious *Helichrysum tepperi* (252) suggest that both species must be basically inbreeders. The low value obtained for *H. tepperi* suggests that female florets usually receive pollen from bisexual florets within the same capitulum. Perhaps female florets are retained because they are one way of enhancing occa-



sional, possibly beneficial, outcrossing. Such a situation has been suggested for inbreeding species of *Lasthenia* (Ornduff, 1966).

It is difficult to comment on the significance of andromonoecy in *H. pygmaeum*. At this stage the relationship of the species is not clear. If derived from an hermaphroditic, self-compatible taxon then it would seem reasonable to assume that the andromonoecious condition is, as commonly suggested, a result of selection for a greater degree of outcrossing. On the other hand Willson (1979) has recently suggested that andromonoecy may be a result of sexual selection, that is that an increase in pollen grain production leads to greater competition between grains to effect fertilization. Whatever the reason for selection further investigation of the breeding systems of *H. pygmaeum* and related taxa is desirable. The P/O value cited was obtained for a single population containing individuals which lack laminae on the capitula bracts and are referable to *H. pygmaeum* var. *occidentale* Benth. Other populations are comprised of individuals with more conspicuous capitula, the bracts possessing white laminae c. 1-2 mm long.

### Evolution, Causes and Consequences of Inbreeding

There is little doubt that inbreeding is generally a derived condition, the evolution of autogamous taxa from predominantly outcrossing taxa being well documented in a large number of families, e.g. *Gilia* (Polemoniaceae: Grant & Grant, 1965, Schoen, 1977), *Leavenworthia* (Cruciferae: Loyd, 1965), *Limnanthes* (Limnanthaceae: Ornduff & Crovello, 1968; Arroyo, 1973) and members of the Onagraceae (Moore and Lewis, 1965; Raven, 1979). Examples within the Compositae include the tribe Cichorieae (=Lactuceae) (Stebbins, 1958), *Lasthenia* (Heliantheae: Ornduff, 1965) and *Eupatorium* (Eupatorieae: Baker 1967). Various attributes of plants support this conclusion (see Stebbins, 1957). For example self-fertilizing taxa often have more specialised morphological characteristics than their outbreeding relative. Furthermore some inbreeders may possess attributes which are of use only in outbreeders e.g. floral markings and non-functional nectaries. Among the other things Stebbins (1957) has also referred to the fact that there are documented records of self-fertilizing populations originating in recent times. This appears to be the case in *Prinula vulgaris* and *Antirrhinum majus*.

Ornduff (1969), when discussing the relationships of reproductive biology to systematics, outlined many character differences which are commonly related to changes from outbreeding to inbreeding. Many such differences, e.g. narrow vs wide distribution, self-incompatibility vs self-compatibility and diploidy vs polyploidy, were observed in a number of Gnaphaliinae (table 2) and generally require no further comment. It is, however, noteworthy that all species with tri- and/or tetramerous disc florets, including those with no apparent outbreeding relative, are inbreeders. Gardner (1977) has pointed out that approximately 80 genera of Compositae contain species with such florets. He suggested that such a change was related to either selective pressure for increased seed production or, as supported here, a change from chasmogamy to autogamy. In some species studies there may well be a correlation of tri- and/or tetramerous florets with an increase in the number of florets and therefore seeds per unit area of receptacle but this factor has not been closely examined.

Possible reasons for selection of inbreeding have been outlined by a number of authors and the various ideas, not necessarily mutually exclusive, have been reviewed by Jain (1976). It has for example commonly been argued (e.g. Grant, 1958; Stebbins, 1958) that inbreeding may be favoured when, under certain environmental conditions, it is advantageous to lower the rate of recombination, thus producing more or less genetically uniform individuals. Other hypotheses include the suggestion that selfing is a mechanism by which a beneficial structural rearrangement in chromosomes may be isolated or is a way in which reproduction may be assured under certain conditions such as a lack of, or competition for pollinators.

Lloyd (1979 a, b) has suggested that there has in fact been over emphasis on the importance of selection for genetic recombination, suggesting instead that factors such as assured reproduction, retrieval of meiotic cost and easier colonization are of greater importance.

While a discussion of the various hypotheses is beyond the scope of this paper the possible importance of pollinator availability is of interest. Arroyo (1972) suggested that autogamy has arisen in *Limnanthes floccosa* as a result of a combination of effects. Thus in the related outcrossing *L. alba*, which sets little seed in the absence of pollinators, the degree to which the species can penetrate into arid regions is dependent on seed production and germination. In exceptionally dry seasons population size is reduced, plants stunted and pollinators scarce or absent. Even following successful pollination ovules often fail to develop because of water stress. On the other hand populations of *L. floccosa* spp. *californica*, which inhabit the same areas as *L. alba*, are little affected by seasonal variation. Because this taxon is autogamous it is not dependent on pollinator activity for high seed set. Furthermore the plants flower much earlier than their outbreeding counterparts, thus enabling ovules to mature before the soil becomes too dry.

In the Gnaphaliinae studied the limited data indicate that some, if not all, of the outbreeding species are self-compatible but the degree of seed set in the absence of pollinators is unknown. Nonetheless a scheme such as that outlined for *Limnanthes* may well explain the selection for a greater degree of selfing in some taxa. On the other hand preliminary observations suggest that none of the species are adapted to specific pollinators, with flies, bees and ants possibly being responsible for the bulk of cross-pollination. In dry seasons the non-dependence on specific pollinators may be an important factor for ensuring pollination. A non-dependence on pollinators is also supported by the fact that outbreeding species of *Angianthus*, plus outbreeders such as *Actinobole condensatum*, *Chrysocoryne pussilla*, *C. uniflora*, *Chrysocoryne* sp. B, *Chthonocephalus* sp.aff. *pseudevax* and other outbreeding species of *Chthonocephalus* commonly occur in as dry or drier regions than their inbreeding counterparts.

Even if pollinator activity has not been an important factor in selection for inbreeding it is nevertheless likely that reproductive assurance has influenced its selection. Indeed, as mentioned above, *Chrysocoryne* sp.C. exhibits both a greater degree of inbreeding and as indicated by field evidence and habit differences, a shorter life cycle than the closely related outbreeder, *C. uniflora*. Although both species inhabit similar environments a greater degree of aridity in the past may well have favoured selection of inbreeding variants with shorter life cycles. Workers such as Solbrig (1976) and Cruden (1977) have suggested that in autogamous species there is a reduction in the amount of energy required for the development of each flower. Waller (1979) has in fact found that cleistogamous flowers of *Impatiens capensis* produce ripe seed in c.24 days compared to c.36 days for chasmogamous flowers. Furthermore it costs about 1.5 to 2 times as much energy, material and time resources to produce outcrossed as opposed to selfed seeds. Thus it would come as no surprise if other inbreeding *Gnaphaliinae* examined were to be found to have a significantly shorter life cycle than their outbreeding counterparts, presumably less energy being required to produce the smaller number of lobes per floret, anthers and/or pollen grains found in these taxa.

The various factors which regulate recombination rates have been thoroughly discussed by Grant (1958) and similarly the genetic consequences have been examined by a large number of workers (e.g. Allard, 1965; Allard et al., 1968; Jain, 1976) and need not be critically discussed. Theoretically inbreeders should be much more homozygous than their outbreeding relatives. However studies have shown that successful inbreeders have extremely flexible genetic systems. On the one hand highly adapted genotypes may be produced to occupy the various microenvironmental niches occupied by a population while on the other the species maintains the ability to adjust to long term changes in the environment. This is in contrast to an

outbreeding species which lacks the ability to perpetuate a highly adapted genotype (Allard, 1965). The distribution of many of the inbreeding species examined across much of the Australian mainland, plus their frequent occurrence in diverse habitats, is perhaps a reflection of this ability. However it should be stressed that inbreeding is of course not a pre-requisite for the successful spread of a species. For example *Chrysocoryne pusilla*, *Millotia myosotidifolia*, *M. greevesii* and some species of *Angianthus* are wide-spread outbreeders. Chromosome number, the possible non-reliance on pollinators and self-compatibility are some factors which may account for their success.

### Distribution Patterns

Given that inbreeding is a derived characteristic the distribution pattern of closely related outbreeders and inbreeders can, like the distribution patterns exhibited by diploid and polyploid entities, provide a clue as to the centre of origin and direction of spread of taxa. In *Actinobole*, *Blennospora*, *Chthonocephalus* and the *Angianthus pygmaeus*/*A. drummondii*/*A. preissianus* group it is tempting to suggest that the inbreeding taxa have been directly derived from their outbreeding relatives. If this is so then it would appear that in all cases, even allowing for some geographical replacement of the outbreeder by the inbreeder, the inbreeding taxa have presumably originated somewhere in Western Australia and subsequently spread to the east.

Disjunct distributions are well known for many species, both plant and animal. For example Green (1964) has cited 35 autochthonous species of flowering plants with marked disjunctions between south-western and south-eastern Australia. Similarly he noted that perhaps c.50 vicarious species pairs of plants existed between the two regions. Most certainly *Chrysocoryne drummondii* is a good example of a species with a disjunct distribution. This species, like *Pogonolepis muellerana* which only appears to occur in the eastern states, has undoubtedly arisen from an ancestral taxon in Western Australia. Detailed distribution maps have not been compiled for species such as *Helichrysum tepperi*, *Helipterum demissum*, *Helipterum pygmaeum*, *Rutidosia multiflora* and *Toxanthes muelleri* but some, if not all, will probably be found to have their otherwise continuous distribution across Australia disrupted in the Nullarbor Plain region.

As pointed out by Green (l.c.) the observed plant disjunctions are unlikely to be the result of a single separation of eastern and western Australia by say the Miocene inundation of the Nullarbor Plain or alternatively late Pleistocene changes. He also pointed out that some disjunctions may well be the result of long-distance dispersal. Several of the species do possess plumose pappus structures which may aid in wind dispersal. Still others frequently occur in saline conditions which suggest that propagules may well tolerate prolonged immersion in sea water. Most certainly *Angianthus preissianus* is likely to be dispersed by sea. Its apparent absence from the coast-line of the Great Australian Bight (fig. 2) may indeed be a reflection of a lack of suitable habitats and/or inadequate collecting in this region. Providing suitable habitats are available then the fact that the above mentioned species are inbreeders also enhances the likelihood of their successful colonization after long distance dispersal, a single plant being capable of establishing a new colony (Baker, 1955).

Many of the species belonging to *Angianthus*, *Blennospora*, *Chrysocoryne*, *Pogonolepis* and other genera examined commonly occur around the margins of salt lakes. Indeed, particularly in *Chrysocoryne*, it would seem that, as well as influencing distribution patterns, the lake systems of south-west Western Australia have been reservoirs for speciation. In this region it is easy to envisage the isolation of populations not only between systems but presumably with any lake system as well. Even today lakes within a system may be isolated for a number of years with water only linking them in exceptionally wet years. For example Bettenay (1962) has traced water movement from Lake Brown to Quairading (Avon System), a distance of approximately 160 km. The very close relationship of the various species of



*Chrysocoryne* suggests that some have evolved in quite recent times. Perhaps the wet-dry oscillations of the past 100,000 years (Bowler, 1980) would provide for the isolation of individual lakes and therefore populations, within any one system. Such oscillations have probably also played an important part in the origin of the inbreeding taxa of *Actinobole*, *Chthonocephalus*, *Pogonolepis* and other genera and may possibly explain the disjunct distributions of many species.

Finally it is of interest to note that Burbidge (1960) suggested that extensive colonization of the arid zone may have occurred from strand habitats. This may well have been the case for the various species of *Angianthus*, *Chrysocoryne* and *Pogonolepis*, all of which contain species occurring in coastal habitats as well as the arid zone. On the other hand, as mentioned above, the genera also contain species commonly found on and often restricted to, the margins of salt lakes. Such distribution patterns do in fact raise the question of whether or not salinity tolerant, ancestral taxa of extant species arose in inland salt lake systems instead of strand habitats. That is, have inland salt lakes also been important reservoirs from which colonization of the arid zone has occurred? At least in *Chrysocoryne* the relationships of the species and their current distribution patterns suggest that such a hypothesis is as equally tenable as a hypothesis suggesting evolution and migration from a strand habitat.

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#### REFERENCES

- Allard, R. W. (1965). Genetic systems associated with colonizing ability in predominantly self-pollinated species. In Baker, H. G. & Stebbins, G. L. (eds.), 'The Genetics of Colonizing Species'. pp. 49-75. (Academic Press: New York).
- Allard, R. W., Jain, S. K. & Workman, P. L. (1968). The genetics of inbreeding populations. *Advances Genet.* 14: 55-131.
- Arroyo, M. T. (1973). Chiasma frequency evidence on the evolution of autogamy in *Limnanthes floccosa* (Limnathaceae). *Evolution* 27: 679-688.
- Baker, H. G. (1955). Self-compatibility and establishment after "long-distance" dispersal. *Evolution* 9: 347-348.
- Baker, H. G. (1959). Reproductive methods as factors in speciation in flowering plants. *Cold Spring Harbor Symp. Quant. Biol.* 24: 177-191.
- Baker, H. G. 1967. The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. *Taxon* 16: 293-300.
- Bentham, G. (1867). Compositae. In 'Flora Australiensis'. 3: 447-680 (Reeve & Co.: London).
- Bentham, G. (1873). Compositae. In Bentham, G. & Hooker, J. D., 'Genera Plantarum'. 2: 163-533. (Reeve & Co.: London).
- Bettenay, E. (1962). The salt lake systems and their associated aeolian features in the semi-arid region of Western Australia. *J. Soil Sci.* 13: 10-17.
- Bettenay, E. & Mulcahy, M. J. (1972). Soil and landscape studies in Western Australia. (2) Valley form and surface features of the south-west drainage division. *J. Geol. Soc. Aust.* 18: 359-369.

- Bowler, J. M. (1980). Age, origin and landform expression of aridity in Australia. Abstract from symposium on "Evolution of the flora and fauna of Arid Australia", Adelaide.
- Burbidge, N. T. (1960). The phytogeography of the Australian region. *Aust. J. Bot.* 8: 75-212.
- Burbidge, N. T. (1963). 'Dictionary of Australian Plant Genera'. (Angus & Robertson: Sydney).
- Cruden, R. W. (1976a). Intraspecific variation in pollen-ovule ratios and nectar secretion—preliminary evidence of ecotypic adaptation. *Ann. Missouri Bot. Gard.* 63: 277-289.
- Cruden, R. W. (1976b). Fecundity as a function of nectar production and pollen-ovule ratios. In Burley, J. & Styles, B. T. (eds), 'Tropical Trees. Variation, Breeding and Conservation.' pp. 171-178. (Academic Press: London).
- Cruden, R. W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.
- Cruden, R. W. & Jensen, K. G. (1979). Viscin threads, pollination efficiency and low pollen-ovule ratios. *Amer. J. Bot.* 66: 875-879.
- Cruden, R. W. & Herрман-Parker, S. M. (1979). Butterfly pollination of *Caesalpinia pulcherrima*, with observations on a psychophilous syndrome. *J. Ecol.* 67: 155-168.
- Eichler, H. J. (1963). Some new names and new combinations relevant to the Australian flora. *Taxon* 12: 295-297.
- Gardner, R. C. (1977). Observations on tetramerous disc florets in the Compositae. *Rhodora* 79: 139-146.
- Gibbs, P. E., Milne, C. & Carillo, M. V. (1975). Correlation between the breeding system and recombination index in five species of *Senecio*. *New Phytol.* 75: 619-626.
- Grant, V. (1958). The regulation of recombination in plants. *Cold Spring Harbor Symp. Quant. Biol.* 23: 337-363.
- Grant, V. & Grant, K. A. (1965). 'Flower Pollination in the Phlox Family'. (Columbia Univ. Press: New York).
- Gray, A. (1851). Characters of some Gnaphalioid Compositae of the division Angiantheae. *Hook. J. Bot. Kew Gard. Misc.* 3: 97-102, 147-153, 172-178.
- Green, J. W. (1964). Discontinuous and presumed vicarious plant species in southern Australia. *J. Roy. Soc. W. Aust.* 47: 25-32.
- Holmgren, P. K. & Keuken, W. (1974). 'Index Herbariorum. Part I. The Herbaria of the World' 6 ed. (Oosthoek, Scheltema & Holkema: Utrecht).
- Jain, S. K. (1976). The evolution of inbreeding in plants. *Annual Rev. Ecol. Syst.* 7: 469-495.
- Lloyd, D. G. (1965). Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contr. Gray Herb.* 195: 3-134.
- Lloyd, D. G. (1979). Some reproductive factors affecting the selection of self-fertilization in plants. *Amer. Naturalist* 113: 67-79.
- Lloyd, D. G. (1979). Parental strategies of angiosperms. *New Zealand J. Bot.* 17: 595-606.
- Merxmüller, H., Leins, P. & Roessler, H. (1977). Inuleae—systematic review. In Heywood, V. H., Harborne, J. B. & Turner, B. L. (eds), 'The Biology and Chemistry of the Compositae'. pp. 577-602. (Academic Press: London, New York & San Francisco).
- Moore, D. M. & Lewis, H. (1965). The evolution of self-pollination in *Clarkia xantiana*. *Evolution* 19: 104-114.
- Mulcahy, M. J. & Bettenay, E. (1972). Soil and landscape studies in Western Australia (1) The major drainage divisions. *J. Geol. Soc. Aust.* 18: 349-357.
- Ornduff, R. (1966). A biosystematic survey of the goldfield genus *Lasthenia* (Compositae: Helenieae). *Univ. Calif. Publ. Bot.* 40: 1-92.
- Ornduff, R. (1969). Reproductive biology in relation to systematics. *Taxon* 18: 121-133.
- Ornduff, R. & Crovello, T. J. (1968). Numerical taxonomy of Limnanthaceae. *Amer. J. Bot.* 55: 173-182.
- Owczarzak, A. (1952). Pollen grains—a rapid method of mounting. *Stain Technol.* 27: 249-253.
- Raven, P. H. (1979). A survey of reproductive biology in Onagraceae. *New Zealand J. Bot.* 17: 575-593.
- Schodde, R. (1963). A taxonomic revision of the genus *Millotia* Cassini (Compositae). *Trans. Roy. Soc. S. Aust.* 87: 209-241.
- Schodde, R. (1968). Further taxonomic notes on the species of *Millotia* Cassini (Asteraceae). *Trans. Roy. Soc. S. Aust.* 92: 27-31.
- Schoen, D. J. (1977). Morphological, phenological, and pollen-distribution evidence of autogamy and xenogamy in *Gilia achilleifolia* (Polemoniaceae). *Syst. Bot.* 2: 280-286.
- Solbrig, O. T. (1976). On the relative advantages of cross and self-fertilisation. *Ann. Missouri Bot. Gard.* 63: 262-276.
- Spira, T. P. (1980). Floral parameters, breeding system and pollinator type in *Trichostema* (Labiatae). *Amer. J. Bot.* 67: 278-284.
- Stebbins, G. L. (1957). Self fertilization and population variability in the higher plants. *Amer. Naturalist* 91: 337-354.
- Stebbins, G. L. (1958). Longevity, habitat and release of genetic variability in the higher plants. *Cold Spring Harbor Symp. Quant. Biol.* 23: 365-378.
- Turner, B. L. (1970). Chromosome numbers in the Compositae. XII. Australian species. *Amer. J. Bot.* 57: 382-389.
- Waller, D. M. (1979). The relative costs of self- and cross-fertilised seeds in *Impatiens capensis* (Balsaminaceae). *Amer. J. Bot.* 66: 313-320.
- Willson, M. F. (1979). Sexual selection in plants. *Amer. Naturalist* 113: 777-790.



## APPENDIX 1

## New Combinations in the Australian Gnaphaliinae

**Actinobole condensatum** (A. Gray) Short, comb. nov.

Basionym: *Gnaphalodes condensatum* A. Gray, *Hook. J. Bot. Kew Gard. Misc.* 4: 228 (1852).

As pointed out by Eichler (1963) the generic name *Gnaphalodes* A. Gray (1852, l.c.) is illegitimate, as it is a later homonym of *Gnaphalodes* Miller (1754). Thus he made a new combination for the species *G.uliginosum*, making the latter the neotype species of *Actinobole* Fenzl ex Endl.

**Blennospora phlegmatocarpa** (Diels) Short, comb. nov.

Basionym: *Calocephalus phlegmatocarpus* Diels, *Bot. Jb.* 35: 614 (1905).

**Pegonolepis muellerana** (Sond.) Short, comb. nov.

Basionym: *Skirrhophorus muelleranus* Sond., *Linnaea* 25: 486 (1853) ('*Muellerianus*').

**Siloxerus pygmaeus** (A. Gray) Short, comb. nov.

Basionym: *Chamaesphaerion pygmaeum* A. Gray, *Hook, J. Bot. Kew Gard. Misc.* 3: 177 (1851).

APPENDIX 2  
**Pollen-ovule ratios of individual populations of species of Gnaphaliinae**  
 (n = number of individuals)

Species	Population	Mean	± Standard Deviation	Pollen-ovule ratio ± Standard Error	n
Actinobole condensatum	Short 380 Red Bluff, W.A. 27°45'S, 114°09'E.	373.6	77.5	20	15
	Short 393 c.100km N. of Murchison River bridge on north-west coastal highway, W.A. c.27°00'S, 114°38'E.	370.3	20.7	12	3
	Short 417 c.28km S. of Overlander Roadhouse on north-west coastal highway, W.A. 26°38'S, 114°33'E.	1,889.8	268.1	77.4	12
	Short 417 c.28km S. of Overlander Roadhouse on north-west coastal highway, W.A. 26°38'S, 114°33'E.	2,155.5	383.5	99	15
	Collections classified as outbreeding or inbreeding on the basis of single P/O values and/or anther size: Outbreeders— <i>Blackall 4695; Burbidge 6464, 6483; Gardner 6038, 6062a, s.n.; Short 4141, 437, 453; Turner 5388</i> . Inbreeders— <i>George 11409; Royce 9680; Storr s.n.</i>				
Actinobole uliginosum	Short 352 c.10km from Three Springs on main Morowa road, W.A. 29°28'S, 115°44'E.	112.5	18.1	4.6	15
	Short 377 c.23km N. of Geraldton on main Northampton road, W.A. c.28°32'S, 114°39'E.	88.5	11.0	2.8	15
	Short 755 c.31.6km E. of Leigh Creek homestead on road to Balcanoona, S.A. c.30°31'S, 138°41'E.	121.8	23.0	5.9	15
	Short 779 Podinna Rock, S.A. 32°41'S, 135°11'E.	127.4	18.9	4.8	15
	Short 864 c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	122.6	12.1	3.1	15
	Barker 2646 c.64km N. of Tibbooburra, Q. 28°56'S, 141°54'30"E.	75.6	18.7	5.6	11
	Short 872 c.4.5km NW of Dimboola, V. 36°26'S, 142°00"E.	117.6	13.2	3.4	11
Short 617 3.4km E. of Meckering in Mortlock River flats, W.A. 31°37'S, 117°02'E.	2,345.4	330.3	85.2	15	
Angianthus pygmaeus	Short 1013 c.14km from Jurien Bay along main road to Badgingarra, W.A. c.30°16'S, 115°07'E.	164.6	28.9	7.4	15
	Short 800 c.10km S. of Streaky Bay on main road to Seeale Bay, S.A. 32°53'S, 134°12'E.	125	19.1	4.9	15
	Short 814 c.7km NE of Wangary on road to Edillilie, S.A. 34°30'S, 135°28'E.	97.3	16.1	4.1	15
Blennospora phlegmatocarpa	Short 908 c.14km W. of Yorketown along main Warooka road, S.A. 35°02'S, 137°28'E.	91.4	17.7	4.5	15
	Short 616 c.3.4km E. of Meckering in Mortlock River, W.A. 31°37'S, 117°02'E.	4,113.5	943.2	243.5	15

Blennospora drummondii	<i>Short 654</i> 5.3km NW of Bruce Rock township on main road to Doodlakine, W.A. 31°52'S, 118°07'E.	4,176.5	766.1	197.8	15
	<i>Short 679</i> Salt depression 1km E. of Wave Rock, W.A. 32°27'S, 118°51'E.	4,069.2	586.8	151.5	15
	<i>Short 318</i> Granitic outcrop c.82.8km WSW of Coolgardie along main road to Perth, W.A. 31°11'S, 120°23'E.	204.2	27.7	7.1	15
	<i>Short 376</i> c.23km N. of Geraldton on main Northampton road, W.A. 28°32'S, 114°39'E.	292.8	30.2	7.8	15
	<i>Barker 4048</i> c.0.75km ENE of summit of Kaiserstuhl, S.A. 34°35'S, 139°00'E.	201	36.5	9.4	15
	<i>Short 815</i> c.17 km from Pt. Lincoln along Flinders highway, S.A. 34°41'S, 135°46'E.	229.8	62.5	16.1	15
	<i>Short 862</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	227.2	50.0	12.9	15
	<i>Chimnock 4335</i> Mt. Walker, W.A. 32°04'S, 118°45'E.	1,932.8	319.8	82.5	15
	<i>Short 924</i> Wangangering Rock, W.A. 31°11'S, 120°31'E.	2,036.2	226.8	58.5	15
	<i>Short 902</i> c.400m W. of Hesso in chenopod shrubland, S.A. 32°08'S, 132°27'E.	1,932.0	365.2	94.3	15
	<i>Short 966</i> 45.1km N. of Koorda along main road to Mollerin, W.A. c.30°28'S, 117°31'E.	2,043.6	278.3	71.8	15
	<i>Short 614A</i> c.3.4km E. of Meckering in Mortlock River, W.A. 31°37'S, 117°02'E.	1,777.5	354.1	91.4	15
	<i>Short 598</i> c.31.3km E. of Dalwallinu on road to Kalannie, W.A. 30°17'S, 116°58'E.	139.0	13.4	3.4	15
	<i>Short 691</i> c.12km W. of Lake King Post Office, W.A. 33°05'S, 119°31'E.	82.6	21.2	5.4	15
	<i>Short 807</i> c.15.2km from Edillilite along main road to Pt. Lincoln, S.A. 34°31'S, 135°40'E.	144.2	21.3	5.5	15
<i>Short 1046</i> c.4.6km E. of Meckering in East Branch of Mortlock River, W.A. 31°37'S, 117°03'E.	105.8	34.3	8.8	15	
<i>Short 605</i> c.4.8km S. of Kondut on main road to Wongan Hills, W.A. 30°45'S, 116°45'E.	41.2	9.4	2.4	15	
<i>Short 614B</i> c.3.4km E. of Meckering in Mortlock River, W.A. 31°37'S, 117°02'E.	51.7	9.3	2.4	15	
<i>Short 632</i> Southern margins of Lake Brown, W.A. 31°07'S, 118°18'E.	52.8	9.2	2.3	15	
<i>Short 394</i> c.100km N. of Murchison River Bridge on northwest coastal highway, W.A. 27°00'S, 114°38'E.	1,539.0	314.0	81.0	15	
<i>Chthonocephalus</i> sp. aff. <i>pseudevax</i>					

## APPENDIX 2 (Continued)

Species	Population	Pollen-ovule ratio			n
		Mean	± Standard Deviation	± Standard Error	
Chithonocephalus pseudevax	<i>Short 322</i> c.12km from Carnamah on main road to Eneababba, W.A. 29°48'S, 115°50'E.	141.2	35.6	9.2	15
	<i>Short 362</i> c.15km from Pindar toward Tardun, W.A. 28°34'S, 115°47'E.	152.9	30.5	7.8	15
	<i>Short 375</i> c.23km N. of Geraldton on main Northampton road, W.A. 28°32'S, 114°39'E.	156.3	26.2	6.7	15
Helipterum demissum	<i>Short 768</i> Carappee Hill, S.A. 32°25'S, 136°16'E.	152.5	23.3	6.0	15
	<i>Short 316</i> Small granite outcrop c.70km WSW of Coolgardie, W.A. c.31°11'S, 120°31'E.	91.8	17.9	4.6	15
	<i>Short 867</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	77.3	15.8	4.0	15
Millotia tenuifolia	<i>Short 861</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	154.9	29.2	7.5	15
Myriocephalus rhizocephalus	<i>Short 813</i> c.7km NE of Wangary on road to Edillilie, S.A. 34°30'S, 135°31'E.	107.6	23.1	5.9	15
Pogonolepis stricta	<i>Short 1053</i> Saline flat running into Leschenault Inlet, c.3km from Bunbury, W.A. c.33°19'S, 115°41'E.	3,185.4	397.7	102.6	15
Pogonolepis sp.A.	<i>Short 372</i> c.13km from Pindar on Pindar-Mullawa road, W.A. 28°31'S, 115°41'E.	3,761.4	516.7	133.4	15
Pogonolepis muellerana	<i>Short 769</i> Waddikee Rocks, S.A. 33°11'S, 135°53'E.	226.3	28.6	7.3	15
	<i>Short 777</i> Margins of Lake Yaminee, S.A. 33°00'S, 135°16'E.	270.8	43.8	11.3	15
	<i>Short 811</i> 4km N. of Cape Tournefort, S.A. 34°55'S, 135°51'E.	160.8	43.4	11.2	15
Toxanthes muelleri	<i>Short 821</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	208.9	23.2	5.9	15
	<i>Short 870</i> As above.	250.8	32.4	8.3	15
	<i>Short 906</i> c.9km from Pt. Wakefield along main road to Ardrossan, S.A. 34°07'S, 138°05'E.	245.4	53.1	13.7	15
Ruridosis multiflora	<i>Short 388</i> The Loop, Murchison River, Kalbarri National Park, W.A. 27°33'S, 114°26'E.	42.3	12.9	3.3	15
	<i>Short 860</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	28.9	7.3	1.9	15
	<i>Short 881</i> c.22km SSW of Casterton, V. 37°47'S, 141°21'E.	29.0	5.5	1.4	15
Helichrysum tepperi	<i>Short 873</i> c.3.2km N. of Douglas on southern margins of North Lake, V. 37°03'S, 141°45'E.	86.0	19.4	5.0	15
Helipterum pygmaeum	<i>Short 868</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	c.37.5	—	—	15
	<i>Short 865</i> c.6km SW of Pt. Julia, S.A. 34°42'S, 137°49'E.	c.252	—	—	15

## APPENDIX 3

## Pair Comparisons of the P/O's of Populations

Populations are designated by the collector's number; see appendix 2.

P = 0.05 or less.

Species	Populations	t	p level	Species	Populations	t	p level	
Actinobole condensatum	417 vs 393	2.113	0.05		862 vs 376	4.35	0.001	
	p.p.				815 vs 376	3.51	0.001	
Actinobole uliginosum	2646 vs 377	2.03	n.s.	Chrysocoryne drummondii	691 vs 598	8.86	0.001	
	2646 vs 352	5.03	0.001		691 vs 807	7.9	0.001	
	2646 vs 872	6.36	0.001		598 vs 807	0.79	n.s.	
	2646 vs 755	5.6	0.001	Chrysocoryne sp.C.	605 vs 614B	3.05	0.001	
	2646 vs 864	7.29	0.001		605 vs 632	3.38	0.001	
	2646 vs 779	6.93	0.001		614B vs 632	0.31	n.s.	
	377 vs 352	4.37	0.001		Chrysocoryne pusilla	902 vs 4335	0.005	n.s.
	377 vs 872	6.5	0.001	902 vs 924		0.94	n.s.	
	377 vs 755	5.05	0.001	4335 vs 924		1.07	n.s.	
	377 vs 864	8.05	0.001	Chthonocephalus pseudevax		322 vs 768	1.02	n.s.
	377 vs 779	6.86	0.001			322 vs 362	0.96	n.s.
	352 vs 872	0.87	n.s.			322 vs 375	1.31	0.01
	352 vs 755	1.23	n.s.			768 vs 362	0.05	n.s.
	352 vs 864	1.79	n.s.	768 vs 375	0.41	n.s.		
	352 vs 779	2.19	0.05	362 vs 375	0.32	n.s.		
	372 vs 755	0.62	n.s.	Helipterum demissum	316 vs 867	2.35	0.05	
	872 vs 864	1.09	n.s.		Pogonolepis muellerana	811 vs 821	3.77	0.001
872 vs 779	1.64	n.s.	811 vs 769			4.87	0.001	
755 vs 864	0.11	n.s.	811 vs 906	4.77		0.001		
755 vs 779	0.71	n.s.	811 vs 870	6.43		0.001		
864 vs 779	0.81	n.s.	811 vs 777	6.9		0.001		
			821 vs 769	6.03		0.001		
			821 vs 906	2.43		0.05		
			821 vs 870	4.07		0.001		
			821 vs 777	4.83		0.001		
			769 vs 906	1.22		n.s.		
			769 vs 870	2.19	0.05			
			769 vs 777	3.29	n.s.			
			906 vs 870	0.33	n.s.			
			906 vs 777	1.42	n.s.			
			870 vs 777	1.41	n.s.			
			Rutidosis multiflora	860 vs 881		n.s.		
				860 vs 388		0.002		
				881 vs 388		0.002		
Angianthus preissianus	908 vs 814	1.04	n.s.					
	908 vs 800	4.97	0.001					
	908 vs 1013	8.32	0.001					
	814 vs 800	4.19	0.001					
	814 vs 1013	7.78	0.001					
800 vs 1013	4.4	0.001						
Blennospora phlegmatocarpa	679 vs 616	0.15	n.s.					
	679 vs 654	0.43	n.s.					
	616 vs 654	0.2	n.s.					
Blennospora drummondii	4048 vs 318	0.27	n.s.					
	4048 vs 862	1.63	n.s.					
	4048 vs 815	1.54	n.s.					
	4048 vs 376	7.49	0.001					
	318 vs 862	1.55	n.s.					
	318 vs 815	1.73	0.05					
	318 vs 376	8.36	0.001					
862 vs 815	0.16	n.s.						



